

PITHING AND MINING BY A PUNKIE: THE UNUSUAL FEEDING STRATEGIES OF *NOLA CILICOIDES* (GROTE, 1873) (NOCTUIDAE: NOLINAE)

Additional key words: *Lysimachia ciliata*, leafmining, plant defense, hypertrophied tactile setae, leaf shelter

Herbivorous insects have evolved innumerable strategies for coping with plant defenses. Among these are efforts made by insects to incapacitate a plant's ability to transport defensive substances through its vascular or lactifer systems to sites of feeding injury. One means of doing such is to trench, vein cut, or otherwise breach the delivery systems of the host so that milky latexes, resins, and gums cannot be transported to the feeding site (Dussourd & Eisner 1987; Dussourd 1993). Another strategy is to girdle the host, either as an adult (e.g., ovipositing females) or as a larva (Forcella 1982; Dussourd 1993; Hanks 1999; Albanese *et al.* 2007). A third option is mass assault: bark beetles are a classic example. Adults attack host trees in such numbers that individuals under siege cannot individually "pitch out" all the invading beetles (Wood 1982). Here we report an example of a fourth option available to herbivores for thwarting a host's defensive system: the hollowing (pithing) of non-woody stem tissues.

In early July 2007 we found young (approximately 3rd instar) larvae of *Nola cilicoides* (Grote) (Noctuidae: Nolinae) pithing upper stems of fringed loosestrife (*Lysimachia ciliata* L.) (Primulaceae). Larvae tunneled into the side of new shoots, removed pith and associated vascular tissues, backed out, then crawled further up the compromised stem to feed on flowers and young leaves.

Nola cilicoides (Fig. 1) occurs from southern Canada to northern Florida and west to Arkansas (Forbes 1960; Handfield 1999; Ferge & Balogh 2000; Covell 2005). In the Northeast the moth is local and uncommon in swamps, floodplains, wet meadows, damp woods, and other mesic to wet community types. Dyar (1899) did not provide life history information for *N. cilicoides* in his study of the early stages of Nearctic nolines. McCabe, in Rings *et al.* (1992), reported that the larva of *N. cilicoides* feeds on new leaves and flowers of fringed loosestrife (*Lysimachia ciliata*). Collection dates for adults in Connecticut and New York normally range from mid June into July, with the occasional specimen taken as early as late May or as late as August and September—we are unsure of the number of generations. In Georgia there are least three full broods (James Adams pers. comm.).

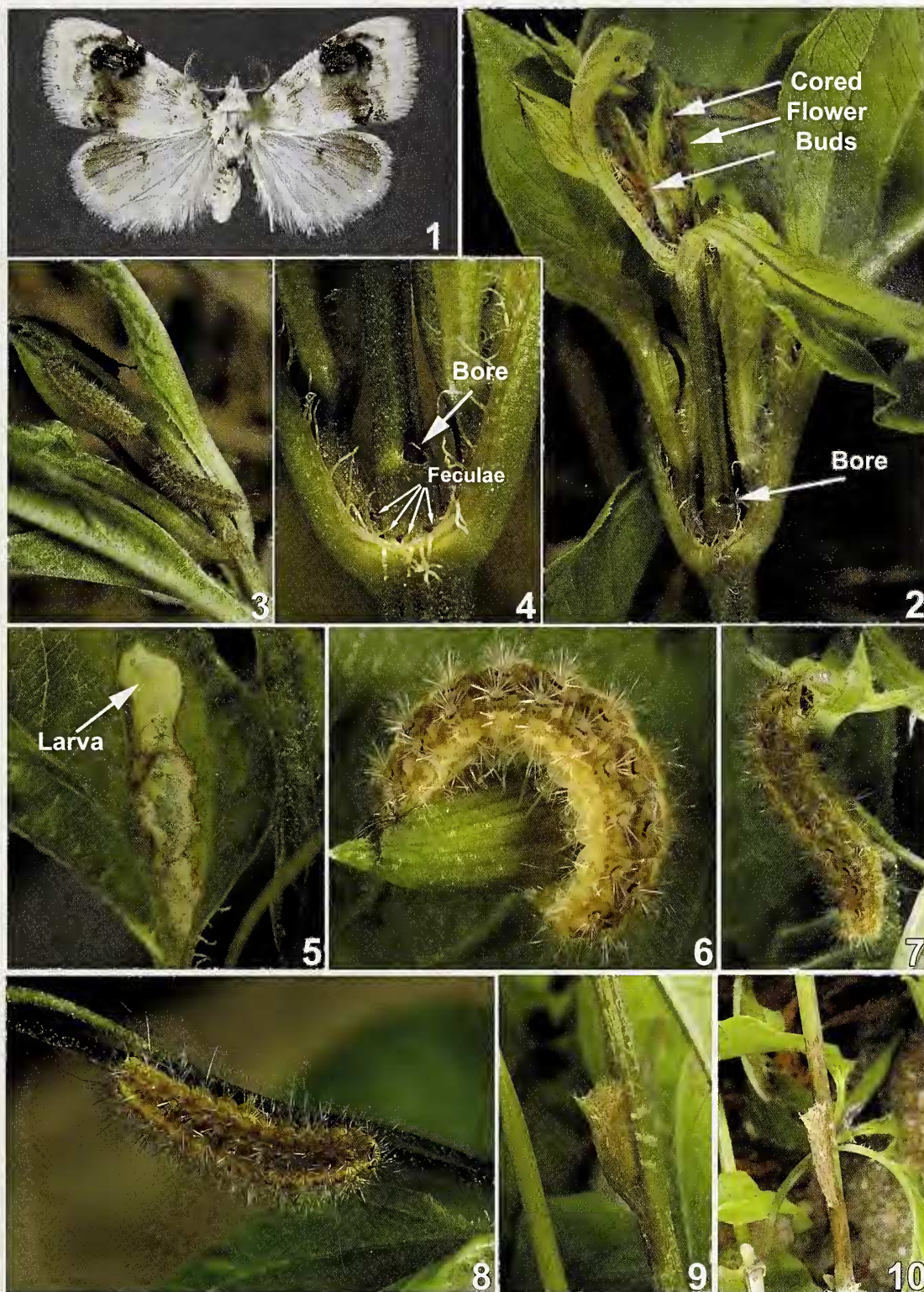
Study Site and Methods. Observations were made

on a colony of *N. cilicoides* located in Lebanon, Connecticut along a powerline cut south of Burnham Road and north of Route 87 (N41° 39' 15.5" W72° 14' 07.6"). Rearing was done in plastic bags and 40 dram plastic vials. Larvae were reared at 21–23° C with photoperiods set to match those outdoors in central Connecticut. Larval and adult vouchers and digital images have been deposited at the University of Connecticut.

Results. On 6 and 11 July, 2007, young larvae of *N. cilicoides* were found feeding on the shoots of fringed loosestrife plants that were coming into flower. Larvae were located by surveying for loosestrife plants with flagging shoots. Each flagged shoot had a small entry hole and small area of cored pith, 5–10 centimeters below the shoot apex (Figs. 2, 4). On each flagged plant, we located 1 or 2 approximately 3rd instar *N. cilicoides* feeding externally (Fig. 3), distal from the wound, on floral buds, flowers, and new leaves. Larvae showed a preference for buds and flowers (Figs. 6, 7) over leaves. Some larvae tied together adjacent leaves and flowers, forming a weak shelter, but silk deposition was sparse and their shelters were poorly defined.

Larval densities were low; only five caterpillars were found on roughly 200 plus fringed loosestrife stems that were searched in early July. In the vicinity of the colony and at other locations in New London and Tolland counties, we searched for, but did not find, larvae on either swamp loosestrife [*L. terrestris* (L.) Britton, Sterns, & Poggenb.] or whorled loosestrife (*L. quadrifolia* L.).

On 9 and 19 August, 2007, we returned to the same stand of fringed loosestrife in Lebanon, ostensibly to look for cocoons. While we failed to find cocoons on more than 60 checked stems, and any evidence on newly bored shoots, we discovered something surprising: young *Nola cilicoides* larvae, 2–3 mm in length mining leaves of fringed loosestrife. Larvae had entered through the lower epidermis, often adjacent to a vein, and then tunneled into the lamina, removing parenchymatic tissues, leaving a full depth blotch mine (Fig. 5). All but one mine had a single entrance/exit hole on the lower leaf surface; the one exception had three entry holes. Dark green to black frass collected in the



FIGS. 1-9. *Nola cilioides* (Grote), all Lebanon, New London Co., Connecticut except adult from Whitefield, New Hampshire. 1. Adult female. 2. Shoot damaged by single larva (arrows point to entry points). Note wilted section of stem above bore hole. 3. Middle instars feeding on young leaves. 4. Detail of 2. 5. Occupied leafmine. 6. Last instar "coring" flower bud with head fully inserted. 7. Last instar feeding on remains of what was previously an open flower. 8. Last instar. While not fully visible, SD setae extend close to all four edges of the image (see text). 9. Cocoon under construction, upper end with abdominal terminus visible. 10. Finished cocoon. Note discolored area of stem above and below cocoon where bark strips were removed.

mine, i.e., little had been expelled. The smallest mine located, was only a few mm in diameter and contained the cadaver of a larva 1.25 mm in length.

In the wild, we found approximately 3rd instar larvae grazing on patches of parenchyma from leaf undersides—scraping away small patches of leaf tissue without feeding through to the upper leaf surface—as late as mid September, indicating that at least some *N. cilicoides* larvae vacate their mines to feed externally, before the onset of winter.

Beginning as early as late August, our captive (lab-reared larvae) spun small, circular to oval, cocoons between overlapping leaves. Cocooned larvae were foreshortened, only 2.6–2.8 mm in length, and evidently had entered a non-feeding diapause in which they would pass the winter. [*Meganola spodia* Franclemont, an oak-feeding noline, also overwinters as a partially grown larva (Butler 1989).]

The full grown larva is 10–12 mm in length (n=8). It is typical for a noline: the prolegs are absent on A3 and secondary setae are present, grouped onto five (dorsal, subdorsal, lateral, subventral, and ventral) warts. Both the dorsal and subdorsal warts have an incomplete black ring around their bases (Figs. 6, 7). The ground color is dirty yellow-orange above, more yellow laterad, and mostly unpigmented below the subspiracular stripe; the creamy to pale orange middorsal stripe is weak over T1. Subdorsal warts on T1–T3 and A7–A9 bear one exceptionally long seta that extends well beyond the body (see below). The head, prominently marked with black (Fig. 7), is drawn into the prothorax at rest.

July-collected, lab-reared larvae formed their pupal cocoons along a stem (Figs. 9, 10), but extensive searches of plants in the wild, including those with wilted tips, did not yield any cocoons. The central chamber of cocoons measured roughly 3 mm x 10 mm. The lower end of the cocoons had an additional 5 mm-long "tail" that tapered downward; the upper end was higher in profile (n=3) (Figs. 9, 10). Like other nolines, numerous strips of stem epidermis "bark" were collected and then woven into the wall of the cocoon. Our caterpillars positioned more than 40 narrow strips of bark, removed from adjacent areas of the stem, into their cocoon walls. Eclosion occurred 1–2 weeks after pupation.

Discussion. The greatly elongated setae that extend from the SD warts at either end of the body of *Nola* larvae (Fig. 8 and caption) presumably serve as an "early warning" system for the larvae. Those issuing from T3 are the longest: in one individual, the longest SD seta extended forward 5.8 mm on a larva only 10 mm in overall length. The rearward-projecting SD seta on A9 of this same caterpillar measured 3.6 mm. In addition,

the subdorsal warts on these segments are oriented in such a way (in living larvae) that the hypertrophied setae are directed well forward on the thoracic and rearward on the abdominal segments. Analogous long dorsal or subdorsal setae also have been reported from choreutids (e.g., *Brenthia*), pyralids (e.g., *Monoloxis*), as well as other noctuids (e.g., *Abablemma* Walker) (Aiello & Solis 2003; Rota 2003, 2008; Wagner *et al.* 2008; Rota & Wagner 2008).

Although *Lysimachia ciliata* has not been investigated, the tissues of other *Lysimachia* species have been found to contain a variety of bioactive compounds including flavonoids, triterpenoid saponins, and phenolic acids (Chang *et al.* 2004). To what degree these are transportable or serve in defense remains unstudied. Our thesis presupposes that *N. cilicoides* larvae tunnel out the pith of their hostplant to incapacitate its vascular tissues—we acknowledge that the pithing behaviors reported here may have little to do with circumventing the plant's ability to translocate antiherbivory substances. Perhaps pithing and the subsequent flagging help the larva to construct its leaf shelter, prevent subsequent growth and maturation of the shoot, enhance survivorship from attacks by natural enemies, or in some other way improve or enhance larval performance or survival. Regardless, the stereotypical behavior is commonly expressed, and stem boring and bud coring represent unique traits for Nearctic nolines, which tend to be rather unspecialized leaf feeders (Forbes 1960; Wagner 2005; Wagner *et al.* 2010).

As noted above, larvae preferentially sought out flower buds and flowers over leaf tissues. A preference for reproductive tissues has been reported for other nolines. *Nola sorghiella* Riley feeds on the seed heads of sorghum and various other grasses and appears to be completely tied to reproductive tissues (our wild-collected larvae failed when offered only leaves). In the Old World, spiny bollworms of the genus *Earias* are major pests of cotton flowers (Pinhey 1975; Kitching & Rawlins 1998).

More surprising was the finding that *N. cilicoides* larvae engage in leaf mining. Leafmining is rare among noctuids. In the East only a handful of apameines mine, and most of these only for the first one or two instars (Wagner *et al.* 2010; Eric Quinter pers. communication). It is exceptional for a "leafminer" to bear secondary setae; more commonly, setae tend to be reduced or absent among leafmining clades (cf. Stehr 1987). We did not observe leafmining behaviors prior to our August visits. Interestingly, life histories with stem mining in spring generations and leafmining in late summer generations have been reported for a number

of European Momphidae (Koster 2002). In North America, *Mompha solomonella* Adamski & Brown, tunnels in shoots of *Cephalanthus occidentalis* L. (Rubiaceae) in the spring, but second and subsequent generations mine leaves (Wagner *et al.* 2004).

Much remains to be elucidated about the biology *Nola cilicoides*. As noted, the selective advantages of pithing and ultimate explanation for this exceptional behavior have yet to be determined. Both observational and controlled studies are needed to better understand the roles of the hypertrophied tactile setae of *Nola* and other lepidopterans. We are also in a quandary about the phenology and broodism of *N. cilicoides* in New England. We were only able document the existence of a single brood—one that produced its pithing larvae in early July. Either we missed a small spring brood, or the partially grown larvae that spun overwintering cocoons in August, waited until early July of the following season to break their diapause.

ACKNOWLEDGMENTS

Tim McCabe, as so many times before, guided DLW's initial efforts. Deane Bowers, Dave Dussourd, Laura McLoud, Jessica McShane, April Rodd, and Bo Sullivan read drafts of the paper. An anonymous reviewer offered many helpful suggestions. Andrea Farr assembled the plates. Both authors were supported on a grant from the CT-Department of Environmental Protection Wildlife Division through the State Wildlife Grants Program; additional support was provided by Northeast Utilities.

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Received for publication 6 Nov 2007; revised and accepted 28 May 2008